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THE EFFECTS OF MICROSITE ON FIRST YEAR ESTABLISHMENT OF WHITE SPRUCE BENEATH ASPEN DOMINATED BOREAL MIXEDWOOD FORESTS

BY

HOWARD BRUCE DELONG (C)

A thesis submitted to the Faculty of Graduate Studies
and Research in partial fulfilment of
the requirements for the degree of
Master of Science

Department of Forest Science

Edmonton, Alberta

Fall 1995

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The effects of microsite on first year establishment of white spruce beneath aspen dominated boreal mixedwood forests

ABSTRACT:

A study was conducted to assess favourable microsites for establishment of Picea glauca (Moench) Voss from seed beneath 40-71 year old Populus tremuloides (Michx) dominated stands in the boreal mixedwood forests of Alberta, Canada. First year establishment, soil strength, root-zone temperature, understory vegetation shading, leaf litter accumulation, and wire (simulating overwintering seedlings) bending were measured on large patches of exposed mineral soil (exposed), small patches of exposed mineral soil (screef), rotting logs (log), mineral soil mounds (mound) and the untreated forest floor (normal).

The mound, exposed and log appeared to be the most favourable seedbeds. Low vegetation cover and high June root-zone temperatures appeared to favour establishment on the exposed seedbed, while moderate vegetation shading, high June root-zone temperatures, and low moist soil strength were related to high establishment on the log and mound seedbeds. Differences in leaf litter accumulation between seedbeds were unrelated to differences in overwinter survival.

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CHAPTER I

INTRODUCTION:

For the first 30 years following clear-cut harvesting in the mixedwood forests of Alberta, regenerated white spruce (Picea glauca (Moench) Voss) may face difficult growing conditions. Plantation establishment is often unsuccessful even with extensive silvicultural effort. This has lead to a renewed interest in mixedwood management and partial cut silviculture systems (Brace and Bella 1988; Navratil et al. 1994). There is a need to understand the microsite conditions that will promote natural establishment of white spruce in the mixedwood understories.

PROBLEMS FOR SEEDLING ESTABLISHMENT ON CLEAR-CUTS:

VEGETATION COMPETITION:

White spruce plantations on clearings frequently suffer from extensive vegetation competition. One to three years after a disturbance, Calamagrostis canadensis (Michx.) Beauv. often overgrows openings (Ahlgren 1960; Blackmore and Corns 1979). Grass heights of 1.1 to 1.7 m may occur (Mitchell 1974). The grass litter, compacted by snow, crushes conifer seedlings (Blackmore and Corns 1979). The litter also acts as an insulator, reducing spring soil temperatures (Hogg and Lieffers 1991).

Trembling aspen Populus tremuloides (Michx) is another main competitor. In Alberta and Saskatchewan aspen stem

densities of 160,000-280,000 per hectare can occur within two years of a disturbance (Bella and De Franceschi 1980). After five years the stem densities are reduced to 50,000-80,000 per hectare. Aspen normally outgrows most tree species.

SNOWSHOE HARE DAMAGE:

Snowshoe hare (Lepus americanus Erxleben) can cause extensive damage to young conifers. Damage is caused by browsing of terminal and lateral leaders of young saplings and by occasional girdling of older saplings (Parker 1984). In summer hares browse on herbaceous material growing in the open but move into denser cover during the winter months (Wolff 1980). White spruce saplings growing in dense young aspen or mixed hardwood stands may be particulary prone to attack (Dyck 1994). These stands appear to act as ideal cover for the snowshoe hare in the winter for thermal and predator protection (Keith 1966; Keith and Windberg 1978; Parker 1984; Radvanyi 1987; Wolff 1980).

CLIMATIC EXTREMES:

White spruce seedlings growing in open exposed conditions are subjected to greater weather extremes in comparison to those seedlings growing in sheltered environments. These extremes may lead to higher seedling mortality in the openings.

I. FROST DAMAGE:

Cold temperatures, occurring at the ground surface, can

cause frost damage on new foliage of conifer seedlings (Christersson and von Fricks 1990). Frost damage may result from ice crystal formation within cells in the seedling (Christersson and Sandstedt 1978) or from photoinhibition and photosynthetic destruction resulting from cold temperatures (Lundmark and Hällgren 1987). In an opening, the seedling is unable to dispose of excess light energy resulting from photoinhibition. Seedlings in the shade receive less light energy and are not as likely to suffer from photosynthetic destruction even if they receive the same cold temperatures as exposed seedlings.

Shelterwood or partial cut systems, in Montana, reduced the occurrence of cold temperatures that lead to frost damage (Hungerford and Babbitt 1987). In the winter, shelter can reduce wind speeds and radiative cooling (Moen 1973). Frost damage on white spruce seedlings in clear-cuts is more frequent than in aspen understories in northeastern British Columbia (DeLong, B.C. Ministry of Forests, unpublished report, 1995).

II. HIGH SURFACE TEMPERATURES

Maximum surface temperatures may be higher in exposed versus sheltered environments (Hungerford and Babbitt 1987). Tree cover reflects and absorbs much of the incoming solar radiation thus reducing surface temperatures (Oke 1978). Örlander et al. (1990) note that temperatures of 50°C are fatal to root cells of conifers. However, they point out that

it is difficult to tell if the damage is due to heat or desiccation, since both occur concurrently.

III. WATER STRESS

Exposed seedlings are more prone to water stress than shaded seedlings. Higher air temperatures are associated with higher absolute humidity differences for any given relative humidity (Grossnickle 1988a). Water is evaporated and transpired out of the needle until the leaf stomata close to avoid water loss.

In the mixedwood forests of Alberta, Marsden et al. (1995) found that absolute humidity differences between the leaf of white spruce foliage and the surrounding air were lower under partial and full deciduous canopies than in clear-cuts during the summer. In a growth chamber study she discovered that low relative humidity was related to reduced net photosynthetic assimilation and water use efficiency of white spruce seedlings.

IV. WINTER DESICCATION:

Winter desiccation can also be a problem for exposed seedlings. Cayford et al. (1959) point out that warm winds in the winter cause drying of the foliage. They state that the foliage suffers a water stress because the tree is unable to take up water, either because the soil or part of the tree itself is still frozen. They observed that winter desiccation of conifers occurred more often in clearings than in un-cut stands. Menzies (Canadian Forest Products, personal

communication, 1994) and Bruhm (British Columbia Ministry of Forests, personal communication, 1994) reported high mortality of planted white spruce in clearings from warm winds during the winter of 1992/93 in the Ft. St. John area of British Columbia. These winds also occur frequently in Alberta mixedwood forests. Under a forest canopy the winds would be reduced and therefore less warming and heat transfer from convection would occur (Oke 1978).

BENEFITS OF MATURING MIXEDWOOD OVERSTORY.

PROTECTION FROM VEGETATION COMPETITION.

Whereas young hardwood stands, that may develop soon after clear-cutting, provide competition to white spruce seedlings, maturing stands are less dense (Bella and De Franceschi 1980) and competition likely becomes less of a factor. Lieffers and Stadt (1994) found that hardwood stands transmit only 14-40% of incoming light, thereby reducing light-requiring vegetation competitors, such as Calamagrostis canadensis, Epilobium angustifolium L., while allowing for sufficient growth of white spruce seedlings. However, they point out that older stands transmit more light and have greater vegetation competition than younger hardwood stands. This suggests that only stands of a moderate age (ie, 40-80 years) would be suitable for controlling vegetation competition while older stands would be unsuitable.

PROTECTION FROM HARE DAMAGE.

As mixedwood stands mature they become taller and more open, no longer acting as shrub habitat for the snowshoe hare. Older stands may again provide favourable habitat as light transmittance increases, leading to higher shrub cover. This suggests that only stands of a moderate age (ie, 40-80 years) are suitable for preventing severe hare browsing.

PROTECTION FROM CLIMATIC EXTREMES:

The shelter of maturing mixedwood stands may offer protection from the weather extremes of exposed sites. White spruce seedling mortality or damage from warm winter winds, vapour pressure deficits, high surface temperatures and frost damage should be reduced from the protection of an overstory.

PROBLEMS FOR NATURAL REGENERATION:

Several studies reveal that natural regeneration of white spruce in undisturbed or partially cut stands of boreal mixedwood forests is inadequate without the aid of site preparation (Kabzems 1971; Lees 1963, 1964, 1970; Quaite 1956).

INADEQUATE MOISTURE DURING DROUGHT:

Place (1955) states that the L and F humus horizons dry too quickly to be a dependable source of moisture during drought and that the seedling's roots must be able to reach to the H layer. In a study in New Brunswick he found that white

spruce seedlings did not penetrate more than 2.5-5.0 cm (at least at light intensities of 20%) in their first year of growth. Therefore, humus with an L+F thickness greater than 5.0 cm may be unfavourable for seedling establishment.

LOW SOIL TEMPERATURE:

Several studies report poor growth of white spruce seedlings at low soil temperature (Brand 1990, Brix 1972; Endean 1972; Goldstein et al 1985; Grossnickle 1987, 1988b; Grossnickle and Heikurinen 1989; Grossnickle and Blake 1985; Kransy and et. al. 1984). Low soil temperature appears to cause a water stress in the spruce seedling by affecting water uptake. Viscosity of water is reduced at low soil temperatures which causes a resistance to water movement (Grossnickle 1988b; Kaufmann 1975). Furthermore, decreases in root permeability of white spruce seedlings, at low temperature, may lead to additional increases in resistance to water flow (Grossnickle 1988b).

Colder soil temperatures can occur beneath the forest floor than in exposed mineral soil during the early growing season (Brand and Janas 1988). Leaf litter has low thermal conductivity, particularly when dry, which reduces the transfer of heat to the mineral soil below (Cochran 1969; Shanks 1956; Stathers and Spittlehouse 1990). Much of the solar radiation absorbed by humus is dissipated as sensible heat back to the atmosphere (Stathers and Spittlehouse 1990).

In addition, the humus and soil may be saturated during

the spring due to a combination of snow-melt and rain. Water has a high heat capacity. In relation to mineral soil, it takes more energy to produce a one-degree celsius change in temperature for water (Cochran 1969; Singer and Munns 1987; Stathers and Spittlehouse 1990). Therefore, saturated soils warm more slowly than drier soils (Cochran 1969; Stathers and Spittlehouse 1990). Low temperatures may be particularly restricting to growth and survival during the early season before soils begin to warm.

LOW LIGHT:

Light may also be limiting to seedlings on the untreated forest floor. At least 20% of full light transmittance is required for conifer seedling establishment (Eis 1970; Shirley 1941). Mixedwood stands dominated by hardwoods have 14-40% light transmittance in the early summer at 1.3 m above the forest floor (Lieffers and Stadt 1994). Only 5.7-6.4% of incident light reaches the forest floor in mixedwood stands during the early summer (Constabel and Lieffers 1995). The reduction in light is attributed to understory vegetation.

LEAF CRUSHING:

Young seedlings that manage to germinate on the untreated forest floor may be prone to shading, smothering and crushing from deciduous leaf litter (Gregory 1966; Koroleff 1954; Rowe 1955; Soos 1967). Many studies have reported adverse effects of forest litter, primarily from trembling aspen and white

birch (Betula papyrifera Marsh.) leaves, on white spruce seedling survival (Day 1964; Day and Duffy 1963; Gregory 1966). Leaf crushing may be the major source of overwinter mortality for white spruce seedlings in their first few years of growth in boreal forest understories (Rowe 1955). Gregory (1966) used cloth screens to protect white spruce seedlings from white birch leaf litter. The screens significantly improved white spruce survival for the first four growing seasons. However, he did not have a replicated experiment.

IMPEDANCE TO ROOT GROWTH:

Conifer root growth and survival may be affected by high soil resistance to root penetration (Zisa et al. 1980). Impedance is highly effected by soil texture and soil moisture. Zisa et al. (1980) reported greater resistances to penetration for silty loam soils than for sandy loam soils at the same bulk densities. Fine textured soils have higher cohesive and adhesive forces, and therefore higher resistance to penetration because of their small grain size and large surface area (Warkentin 1984).

Resistance to penetration tends to increase with decreasing soil moisture (Eavis 1972; Ehlers et al. 1983; Warnaars and Eavis 1972). Water films may provide lubrication (Lull 1959) that allows for particle rearrangement and lower resistances to penetration when soil is moist. Soil resistance to penetration may reduce white spruce establishment on fine textured soils during periods of drought

when soil water is depleted. Soil resistance to penetration is termed soil strength.

POTENTIAL ADVANTAGES OF ROTTING WOOD AS A SEEDBED:

Rotten wood appears to be the best microsite for initial establishment of white spruce regeneration in undisturbed stands and shaded microsites (Day 1963,1964; Day and Duffy 1963; Griffith 1931; Hellum 1972; Hughes 1967; Lees 1964,1970; Phelps 1948; Rowe 1955). In southwest Alberta, decayed wood supported 42% of the conifer regeneration of conifers but represented only 3% of the area (Day 1964).

IMPROVED MOISTURE DURING DROUGHT:

Several studies report high moisture content in rotten logs (Barr 1930; Harvey et al. 1987; Harvey et al. 1978; Jurgensen et al. 1984; Larsen et al. 1978; McFee and Stone 1966). Moisture contents of decayed wood increase with advancing stages of decay (Barr 1930; Jurgensen et al. 1984; Larsen et al. 1978). Therefore, rotting wood in the later stages of decay may be a favourable microsite for white spruce establishment during periods of drought.

IMPROVED ROOTING TEMPERATURE:

There is little information about the rooting temperature of rotting wood. In Norway forests the surface temperature of rotted stumps and windfalls always have higher mean diurnal germination layer temperatures than that of the soil (Olsen 1934). Day (1963) found that on a hot day in the Rocky

mountains of Alberta, shaded, decayed coniferous wood had lower diurnal temperatures, at 7 cm depth, than shaded sandy loam soil and soil from an Ah horizon. Temperatures were similar to F and H humus. There was little difference in surface temperature amongst the four seedbeds. However, these reflect hot conditions in summer. The results may be quite different for seedbeds in the boreal forest during a cool, wet, spring.

During cool springs in the boreal forests, rotting wood may have higher rooting temperatures than other microsites. This may be due to a lower water content than other microsites which may be saturated (the reverse may occur later in the season as other microsites dry and the rotting logs remain moist). Rotting wood has high microporosity and a curved surface which should allow for some water drainage. Also, the elevated position may allow for more exposure to the sun, leading to faster snow-melt and increased water evaporation.

IMPROVED LIGHT:

Rotting wood may be a favoured microsite for white spruce establishment because it is generally associated with gaps in the forest canopy and improved light conditions (Rowe 1955). Rotting wood would also provide an elevated microsite over shading understory vegetation. This may allow just enough light for white spruce establishment.

PROTECTION FROM LEAF CRUSHING:

Leaf litter has a tendency to be swept off the tops of small ridges and hummocks (Koroleff 1954) such as rotten logs. Higher white spruce establishment on rotting logs in boreal forests may be partially due to lower mortality from leaf litter crushing and smothering (Rowe 1955).

LOWER ROOT IMPEDANCE:

Rotting wood may have low resistance to penetration compared to mineral soil. Rotting wood has a low bulk density (Penka and Červená 1984) and resistance to penetration generally decreases with a decline in bulk density (Eavis 1972; Ehlers et al. 1983; Jayawardane and Blackwell 1990; Zisa et al. 1980). Rotting wood also has high macroporosity. This may mean it has low cohesive and adhesive forces that would limit root penetration.

POTENTIAL ADVANTAGES OF EXPOSED MINERAL SOIL AS A SEEDBED:

Exposed mineral soil may also be a favourable seedbed in the understory, perhaps even more so than rotting wood. However, exposed mineral soil rarely occurs naturally underneath boreal hardwood forest canopies. Several experiments have reported higher germination and survival of white spruce on artificially exposed versus untreated soils in mixedwood or white spruce stands (Ackerman 1957; Crossley 1949; Kolabinski 1994; Lees 1963, 1964, 1970; Phelps 1948; Quaite 1956; Rowe 1955; Waldron 1966; Youngblood and Zasada

1991, Zasada and Grigal 1978; Zasada 1990).

IMPROVED MOISTURE DURING DROUGHT:

Removal of the humus layer should increase the moisture available to seedlings during drought periods. The upper horizon of mineral soil should dry less quickly than the humus layers (due to smaller pore size and retention of water through hydrogen bonding).

IMPROVED ROOTING TEMPERATURE:

Removal of the insulating humus layer would be expected to increase soil temperatures. However, temperatures may still be cold under saturated conditions.

IMPROVED LIGHT:

Removal of understory vegetation would increase the amount of sunlight reaching the surface. This may be adequate for white spruce seedlings.

POTENTIAL ADVANTAGES OF MINERAL SOIL MOUNDS AS A SEEDBED:

If rotting wood and exposed mineral soil are good seedbeds it is possible that mineral soil mounds might also be favourable as it combines properties of both of these two seedbeds.

IMPROVED SOIL TEMPERATURE:

The lack of an insulating humus layer, the increased surface area, and the elevation above understory vegetation and melting snow should increase average soil temperatures on

a mineral soil mound. Also mounding (and other forms of cultivation) can decrease soil porosity (Cochran 1969) and improve soil drainage (Stathers and Spittlehouse 1990) which would also increase soil temperatures during wet springs.

IMPROVED LIGHT:

The removal of vegetation and the increased elevation of the mound may allow enough sunlight for adequate growth of white spruce seedlings.

PROTECTION FROM LEAF LITTER DAMAGE:

The elevation and curvature of the mound should allow for leaves to be swept or blown off.

LOWER ROOT IMPEDANCE:

Mixing of soil (such as mounding) reduces bulk density, at least temporarily, which lowers soil impedance to root growth (Ehlers et al. 1983; Jayawardane and Blackwell 1990). Mounding increased light, soil temperature, aeration, and nutrient uptake on cold wet soils on a clear-cut in the interior of British Columbia (Spittlehouse et al. 1990). In addition five year planted seedling survival and growth was better than on untreated ground.

OBJECTIVES:

There are numerous reports that document problems that can affect white spruce seedling establishment in the understory of hardwood stands, but there are few that measure

each problem and compare them amongst different seedbeds. This study had three objectives:

1. Determine differences in first summer seeded establishment (germination and survival) and planted germinant survival of white spruce seedlings between various seedbeds: rotting wood, mineral soil mounds, large patches of exposed mineral soil, small patches of exposed mineral soil, and the undisturbed forest floor.

2. Determine differences between seedbeds in vegetation shading, root-zone temperature, soil moisture, soil strength, and leaf litter accumulation.

3. Determine the association of vegetation shading, root-zone temperature, soil moisture, and soil strength, with first summer seeded establishment and planted germinant survival.

4. Determine seedbed differences in first year overwinter survival of white spruce seedlings established form seed and planted germinants.

5. Determine the association of leaf litter accumulation with overwinter survival of seedlings established from seed and planted germinants.

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CHAPTER II
The effects of microsite on first summer seeded establishment and planted germinant survival of white spruce beneath aspen dominated boreal mixedwood forests.

INTRODUCTION:

Recently there has been renewed interest in mixedwood management and partial cut silviculture systems in the boreal forests of Alberta (Brace and Bella 1988; Navratil et al. 1994). One of the objectives is to promote and take advantage of natural regeneration of white spruce (Picea glauca (Moench) Voss) in the understory. A significant question is what are the microsite conditions that will promote natural establishment of white spruce in the understory?

Natural regeneration or artificial seeding on the forest floor, in boreal mixedwood forests, has limited success (Crossley 1949; Day 1963; Griffith 1931; Kolabinski 1994; Youngblood and Zasada 1990; Lees 1963,1964, 1970; Waldron 1966). Reduced light transmittance from understory shading (Constabel and Lieffers 1995) can retard germination (Carlson 1983) and growth (Eis 1970; Shirley 1941). Low soil temperatures created by the insulating effect of the forest floor (Brand and Janas 1988) may also reduce seedling growth (Goldstein et al. 1985; Grossnickle 1987; Grossnickle and Blake 1985). Low temperatures may become less of a factor as soils warm during the growing season. First year seedlings growing on the forest floor may be prone to drought since the top litter layers dry out quickly (Place 1955). Root growth

and survival may be impaired by high soil resistance to root penetration (Zisa et al. 1980). Resistance to penetration can increase greatly with decreasing soil moisture (Eavis 1972; Ehlers et al. 1983; Warnaars and Eavis 1972).

Rotting logs (Day 1964, 1963; Griffith 1931; Lees 1972) and exposed mineral soil (Crossley 1949; Dyck 1994; Kolabinski 1994; Lees 1963, 1964, 1970; Rowe 1955; Waldron 1966; Youngblood and Zasada 1990) appear to be the best seedbeds (microsites) for natural regeneration of white spruce in undisturbed or partially cut conifer or mixedwood stands.

Possible reasons for higher establishment on exposed seedbeds include: reduced vegetation competition and increased moisture at the surface during drought (Ackerman 1957; Crossley 1949; Quaite 1956; Waldron 1966). In addition, removal of the insulating humus layers should elevate soil temperatures and improve seedling establishment.

Potential advantages of rotting logs for white spruce establishment are: higher moisture retention in periods of drought, increased light conditions, reduced vegetation competition, and higher rooting temperatures (Barr 1930; Day 1963; Lees 1972; Place 1950; Rowe 1955). In addition, rotting logs should have lower resistance to root penetration. Rotten wood has low bulk density (Penka and Červená 1984) and resistance to penetration generally decreases with a decline in bulk density although other factors are also involved (Eavis 1972; Ehlers et al. 1983; Jayawardane and Blackwell

1990; Zisa et al. 1980).

If rotting wood and exposed mineral soil are appropriate seedbeds it is possible that mineral soil mounds might also be favourable as they combine properties of both of the other two seedbeds. Mounding increased light levels at the soil surface, soil temperature and nutrient uptake on clearings (Spittlehouse et al. 1990). Mounds would likely have reduced impedance to root growth because soil mixing reduces bulk density, which at least temporarily lowers impedance (Ehlers et al. 1983; Jayawardane and Blackwell 1990).

There are numerous reports of the physical factors that affect white spruce seedling establishment in the understory of hardwood stands, but there are few that measure each factor and compare them amongst different seedbeds. This study had three objectives:

1. Determine differences in first summer seeding establishment (germinantion and survival) and planted germinant survival of white spruce seedlings between various seedbeds: rotting wood, mineral soil mounds, large patches of exposed mineral soil, small patches of exposed mineral soil, and the undisturbed forest floor.
2. Determine differences between seedbeds in understory vegetation shading, root-zone temperature, soil moisture, and seedbed strength.
3. Determine the association of vegetation shading, root-zone temperature, soil moisture, and seedbed strength, with

first summer seeding establishment and planted germinant survival.

MATERIALS AND METHODS:

SITE SELECTION AND DESCRIPTION:

Four sites were chosen for the study near Whitecourt Alberta. All sites were more than 5 km apart. Each was contained within the lower boreal cordilleran (LBC) ecoregion (Corns and Annas 1986). A description of each site is given in Table 2-1. Each site was 100 × 100 m with a 60 m wide forested buffer zone around the perimeter. There were at least 10 rotting logs of either white spruce, trembling aspen (Populus tremuloides (Michx)), or balsam poplar (Populus balsamifera L. ssp balsamifera) (at least 10 cm in diameter, a minimum of 10 centimetres above the forest floor at surface of the rooting wood, and in decay classes III or IV (Maser et al. 1988)). Conifer seedlings are found more often on logs of advanced decay than on those with low decay (McCullough 1948). Germination and survival of white spruce is similar on decayed trembling aspen and white spruce logs, but inferior on white birch (Betula papyrifera Marsh.) logs (Hellum 1972). Therefore, white birch rotting logs were not considered to be acceptable.

All sites chosen were in 40-71 year old stands with a predominant trembling aspen overstory (Table 2-1). White spruce seedlings in younger hardwood stands are subject to

severe browsing from snowshoe hare (Lepus americanus Erxleben) (Dyck 1994). The young hardwoods act as shrub cover for thermal and predator protection in winter (Keith 1966; Keith and Windberg 1978; Parker 1984; Wolff 1980). Younger stands also have low light transmittance in summer, both at the forest floor (Constabel and Lieffers 1995) and at slightly elevated positions (Constabel and Lieffers 1995, Lieffers and Stadt 1994). Older stands have more light transmittance which can result in increased competition from Calamagrostis canadensis and shrubs (Lieffers and Stadt 1994). High shrub cover, associated with older stands, may also act as favourable habitat for the snowshoe hare, leading to browsing mortality. Therefore, 40-70 year old mixedwood stands may be the most suitable for understory establishment.

PLOT DESCRIPTION:

There were four sites, each which contained 10 plots and five seedbeds per plot. The seedbeds were: rotting logs (log), large patches of exposed mineral soil (exposed), small patches of exposed mineral soil (screef), mineral soil mounds (mound), and the undisturbed forest floor (normal). Ten rotting logs were randomly chosen at each site. On each log a 2 m length was randomly selected and the middle of this length constituted a plot centre. The centres of the other four seedbeds were randomly assigned to one of four locations that were 1.2-2 m in a perpendicular direction from the 0 and 2 m ends, on either side of the log.

The exposed mineral soil seedbed was formed by removing all brush, roots, and litter down to 5 cm in depth in a 2 m diameter.

The screef mineral soil seedbed was created by removing all brush, roots, and litter down to 5 cm in depth in approximately 10 × 10 cm patches for a total of 10 patches per seedbed. The patches were arranged in a circular pattern with a 1 m radius. This seedbed exposed mineral soil but left some of the understory shrubs and herbs intact.

The mound seedbed consisted of two mounds, 80 cm in diameter and 40 cm high, built of mineral soil (A and B horizons) on top of an intact forest floor. Herbs and shrubs were removed where required. The mounds were hand-dug using soil adjacent to the plot.

The normal forest floor consisted of the unaltered forest floor including an intact cover of herbs and shrubs.

SEEDLING PRODUCTION:

White spruce seed of a Whitecourt provenance was soaked for 24 hours, stratified for three weeks at 5°C and planted in styro miniblocks (Beaver Plastics Ltd., Edmonton, Alberta). Each block was 60 × 35.25 cm with 448 cavities. Cavities were 2 cm in diameter and were originally 7 cm deep. The depth was reduced to 3.5 cm by cutting the miniblocks in half. The cavities were filled with peat. Three to four seeds were placed in each cavity and tamped into the peat. The miniblocks were placed in a greenhouse in March, 1993 to allow

for seed germination. The blocks were watered as required to maintain the peat near field capacity. The water contained a fertilizer of 20-20-20 $N-P_2O_5-K_2O$ (0.30 grams per litre of water). The seedlings were grown for six weeks. Acceptable germinants had at least 0.5 cm of needle bearing stem and no visible chlorosis.

FIELD ESTABLISHMENT :

During May 1993, six white spruce germinants and four groups of 23 pre-stratified seeds (except for site four with 15 seeds per group), of 65% known viability, were randomly located on each seedbed.

FIELD MEASUREMENTS:

Thermocouples were inserted in the centre of each seedbed, at a depth of 7 cm, and temperatures were assessed with a multimeter and ice point junction. Temperatures were taken between 14:00 and 16:30 hours on June 30 and June 31, 1993, and again on August 12 to August 17, 1993.

Soil strength (includes rotten log) was estimated using a cone penetrometer (Star Quality Samplers, Edmonton, Alberta). Penetration resistance of a penetrometer correlates well with the resistance of the soil to root penetration (Barley et al. 1965; Sands et al. 1979; Taylor and Ratliff 1969). Three different rod diameters were used depending on the soil strength. The rod was pushed into the seedbed to a depth of 10 cm with a steady downward force for a period of

approximately five seconds. The amount of displacement on the plunger was a measure of the seedbed resistance or strength. This was expressed in KPa.

Strength sampling was done within two to three days of precipitation in June and August 1993 (moist) and again during drier periods (a week or more without precipitation) in July and September 1994 (dry). Only sites two and four were sampled in the dry periods.

Water potential readings were taken during the dry weather periods of July and September, 1994, for sites two and four only. Measurements were made by placing thermocouple psychrometers (Wescor Inc., Logan, Utah) in the middle of each seedbed, at a depth of 5-10 cm, allowing them to equilibrate for 3 hours, and then reading the voltage and temperature from a microvoltmeter. Microvoltage was adjusted to equivalent readings at 25°C by applying the equation:

$$Corrected\ reading = \frac{Observed\ reading}{0.325 + Observed\ Temperature}$$

Water potential was then expressed as MPa by dividing by -4.7.

An ocular estimate of percent vegetation cover (shrub and herbaceous cover, less than 2 m in height, within a 2 m radius, that would occur within a 90° inverted cone) was made from August 10 to August 12, 1993.

First year establishment was recorded in September 1993 prior to leaf-fall. An individual group of 23 (15 on site

four) seeds was considered established if at least one seedling had germinated and survived. Each group or seedling, on a seedbed, were recorded as dead or alive, with the condition of live seedlings being classified as dead, poor, medium or good. Seedlings that were in very poor shape and were not expected to survive for more than a month were classified as dead.

STATISTICS:

Analysis of variance, using the GLM (SAS Institute Inc. 1989) procedure was used to determine seedbed effects on early and late season temperatures, percent vegetation cover, and moist and dry soil strength. A randomized block design was chosen with plots nested within sites (Table 2-2). The experimental unit was the seedbed × plot within site. Sites and plots were random effects and seedbed was fixed.

Transformations according to the Box and Cox (1964) procedure were applied to root-zone temperature (August 1994) (power of -1.6), percent vegetation cover (power of 0.35), soil strength (moist) (natural log), and soil strength (dry) (power of 0.24). The method is as follows:

$$y^{(\lambda)} = \frac{y^{\lambda} - 1}{\lambda \ddot{y}^{\lambda - 1}}, \qquad (y^{(0)} = \ddot{y} \ln y)$$

Where y is a single observation, $\ddot{y}$ is the geometric mean of all observations, and λ is a particular transformation. Through maximum likelihood estimation, a λ is chosen so that

the error terms; plot(site), site×seedbed, and plot(site)×seedbed for $y^{(4)}$ are minimized.

Where there were significant main effects, the Ryan-Elinot-Gabriel-Welsch multiple F test (Elinot and Gabriel 1975) was used to test for differences amongst means at α = 0.05.

If a response variable had been transformed, all analyses were applied on the transformed data. For illustrative purposes all transformed means were back-transformed as geometric means. Approximate standard errors were applied to the geometric means through procedures given in Høj et al. (1993). The procedure is as follows:

$$Sx = (\hat{Y} \pm S\hat{x})^{\text{Inverse transformation}} - \hat{Y}^{\text{Inverse transformation}}$$

Where Sx is the revised approximate standard error, $\hat{y}$ is the transformed mean, and $S\hat{x}$ is the transformed standard error. Since the revised standard errors are not symmetrical about the geometric mean, both the positive and negative values are given.

Logistic regression, using the LOGISTIC (SAS Institute Inc. 1989) procedure was applied to all survival data. The independent variables seedbed, site, root-zone temperature (June 1993), root-zone temperature (August 1993), soil strength (moist), and vegetation cover were assessed to find the model that best estimated first summer seeded establishment and planted germinant survival. Data were

combined across plots to produce adequately large counts for analysis. Where site or seedbed effects occurred, all possible comparisons were made using Wald Chi-Square probabilities and a modified Bonferroni approach (Holm 1979). Probabilities were ordered from smallest to highest. Significance for a particular comparison was determined based on the following criteria:

$$p_{(i)} > \alpha/(k-i+1)$$

Where $P_{(i)}$ is the probability of the ith comparison, k is the number of comparisons made, and $\alpha = 0.05$. When $P_{(i)}$ was greater the null hypothesis was not rejected.

Logistic regression was used to test for significant relationships between first year establishment and each of: root-zone temperature (June 1993), root-zone temperature (August 1993), percent vegetation cover, and soil strength (moist).

RESULTS:

There were significant seedbed effects for all of the physical variables measured ($P < 0.01$) (Table 2-3). In addition, there were significant site and site × seedbed effects for August 1993 root-zone temperature, and moist and drier soil strength ($P < 0.01$). The seedbed comparisons of temperatures for June 1993 and August 1993 were similar (Figure 2-1(A,B)). The mound had the highest temperatures (13.4°C and 15.0°C for June and August respectively) while the

normal (8.8°C and 11.2°C), and screef seedbeds (8.8°C and 11.0°C) had the lowest temperatures.

The exposed seedbed had the lowest vegetation cover (4.6%) while the normal seedbed had the highest cover (29.4%). The mound, log, and screef seedbeds had intermediate vegetation cover. The log (20.0%) had significantly greater cover than the screef seedbed (13.4%), but was not significantly different from the mound seedbed (14.0%).

There are some similarities between soil strength measurements taken under moist and drier conditions (Figure 2-1(C,D)). The log (109 KPa) and the mound (151 KPa) had the lowest moist strengths. The log had the lowest dry strength (165 KPa) while the mound tended to have lower (792 KPa) dry strengths than the other three seedbeds. The exposed (470 KPa), normal (495 KPa), and screef seedbeds (678 KPa) had the highest moist soil strengths. This was also true for the dry soil results, although the strengths of the exposed (1,547 KPa) and screef (1,835 KPa) seedbeds were considerably higher than that for the normal seedbed (1,003 KPa). Also, the strengths for the normal and mound seedbeds were similar which was not observed in the moist soil comparisons.

Water potential was measured but is not reported. Readings were highly inconsistent. This is likely due to high temperature fluctuations near the surface which in turn caused vapour pressure gradients within the psychrometer (Brown and Oosterhuis 1992).

Logistic regression analysis of first summer survival indicated that a seedbed×seedling effect contributed significantly to the fit of the model ($P < 0.001$) (not shown). Therefore, the first summer survival of planted germinants and the establishment of seeded germinants were analyzed separately.

Logistic regression analysis of first summer survival of planted germinants (Table 2-4) shows that the best fitting model includes site, seedbed, site×seedbed interactions, and moist strength effects ($P < 0.025$). Seedbed comparisons for each site were made using this model. The probability of seedling survival on the screef and mounds seedbeds (Figure 2-2(A)) were low and high respectively on all sites (though not always significant). It also appeared that the normal seedbed had a lower probability of survival than the log, mound, and exposed seedbeds (but only significant on site two).

Percent vegetation cover did not appear to be related to planted germinant survival (Table 2-5). Although temperatures in August and late June did not contribute to the best fit logistic model for planted germinant survival (Table 2-4) they were both significant (Table 2-5) ($P = 0.0001$ for June, and 0.012 for August) when no other effects were in the model. There was a trend for increasing survival with increasing June (Figure 2-3(A)) and August (Figure 2-3(B)) temperatures.

When seedbed and site effects were included, the addition of June ($P > 0.500$) or August ($P > 0.950$) temperature to the

model is no longer significant. It appeared that most of the June and August temperature relationship to planted germinant survival was explained by site (between) and seedbed (between) differences in June and August temperature. The mound, log, and exposed seedbeds had higher June temperatures and tended to have higher planted survival then the screef and normal seedbeds, although this varied with site. The same pattern appeared to be occurring for August temperatures. However, many low August temperature-low planted survival observations occurred on the screef seedbed (Figure 2-3(B)). When these observations are removed the relationship of August temperature to planted survival is no longer significant ($P > 0.394$). Therefore, August temperature may not have been important to planted survival.

There was a trend of increasing planted germinant survival (Figure 2-2(A)) with decreasing moist soil strength (Figure 2-3(C)). The relationship of strength to survival (Table 2-5) was highly significant ($P = 0.0001$) when no other effects were included in the logistic model. When seedbed, June temperature, and seedbed × temperature interactions are included in the model, the addition of moist soil strength is no longer significant ($P < 0.001$). This suggests that the relationship of moist soil strength to planted germinant survival is largely explained by seedbed (between) differences in moist soil strength, a June temperature relationship to soil strength, and June temperature × seedbed (between)

interactions. The mound and log seedbeds had lower moist soil strength than the normal and screef seedbeds and tended to have higher planted survival. The exposed seedbed had high moist strength but also tended to have high survival. The June temperature of the exposed seedbed was higher than the screef and normal seedbeds (Figure 2-1(A). The relationship of June temperature to moist soil strength may explain the higher survival on the exposed seedbed. In comparison to the screef and normal seedbeds, higher temperatures on the exposed seedbed may have allowed for better root penetration and survival.

When June temperature, August temperature, and moist soil strength are included as a group in the model for planted germinant survival, (Table 2-5) the addition of site ($P < 0.001$), seedbed ($P < 0.001$) and site×seedbed ($P < 0.010$) effects are still significant. This indicates that there were other environmental factors related to planted germinant survival that were a result of site (between), seedbed (between) and site×seedbed (between) interactions.

Logistic regression analysis of first summer seeded establishment (Table 2-4) revealed that only seedbed and site contribute significantly to the model ($P < 0.001$). The interaction term did not significantly improve the prediction of seed establishment ($P > 0.100$). Seedbed comparisons were made using the unsaturated model containing only the seedbed and site effects. Multiple comparisons (Figure 2-2(B))

indicate that the probability of establishment was lowest on the normal seedbed but that this was not significantly different from the mound and screef seedbeds. The probability of establishment on the exposed seedbed was greater than that for the screef, normal, and mound seedbeds but was not significantly different from the log seedbed. The probability of establishment was not significantly different for the mound, log and screef seedbeds.

June temperature, August temperature and moist soil strength did not appear to be related to seed establishment. Although percent vegetation cover did not contribute to the best fit logistic model for seed establishment (Table 2-4) it was significant (Table 2-5) ($P = 0.0003$) when no other effects were in the model. There was a trend for increasing survival with decreasing vegetation cover (Figure 2-3(D)).

When seedbed is in the model for seeding establishment (Table 2-5), the addition of vegetation cover is no longer significant ($P > 0.25$). This suggests that the relationship of vegetation cover to seeding establishment could be explained by seedbed (between) differences in vegetation cover. The exposed seedbed had the lowest vegetation cover (Figure 2-1 (E)) and the highest seeding establishment (Figure 2-2 (B)), whereas, the normal seedbed had the highest cover and the lowest establishment. The mound, log, and screef seedbeds had both intermediate vegetation cover and establishment.

When vegetation cover was included in the model (Table 2-5) for seed establishment the addition of site, and seedbed effects were still significant ($P < 0.005$). This indicates that there were other environmental factors related to seed establishment that were influenced by site (between) and seedbed (between) differences.

The lowest probability of survival for both planted survival and seed establishment occurred on site two. The average planted survival on all seedbeds was 26.3% on site two, compared to 70.7% on site three, and 57.3% on sites one and four. The seeding establishment on site two was 28% compared to 40.5% for site one, and 48% for sites three and four each. It was noted that site two had the highest crown cover (Table 2-1) and leaf area index (chapter III).

It was observed that some mortality on the seedbeds, for both planted and seeded germinants, took place due to litter smothering. Loose litter from previous years was blown by wind and settled on many of the seedlings. This was particulary evident on the screef seedbed. It was also noted that some mortality on the mound seedbed (particulary for seeded germinants) was due to soil erosion from rain.

DISCUSSION:

The combination of low to intermediate vegetation cover, high June root-zone temperatures and low resistance to root penetration appear to be favourable for first year germination

or survival of white spruce seedlings on the mound and log seedbeds beneath aspen dominated forests. The seeding establishment on the mound seedbed could have been improved if the seed were deposited on surfaces where rain erosion would be less damaging. Low vegetation cover and a high June root-zone temperature may favour white spruce germination and survival respectively on the exposed seedbed. The screef and normal seedbeds appear to be unsuitable.

High vegetation cover may have caused reduced seeding establishment by decreasing the amount of available red light. Red light is thought to stimulate conifer seed germination if the seed has not been properly stratified (Carlson 1983). The seed in this experiment was not pre-stratified.

Vegetation cover was not related to planted germinant survival but it may still have had an impact on growth of the seedlings. Brix (1972) and Durzan (1971) reported increased growth of white spruce seedlings with increased light. The normal seedbed may have had reduced growth due to restricted light.

The lack of a temperature relationship with seeded establishment may be because initial seedling growth is dependent on seed reserves (Kramer and Kozlowski 1979) and may not be affected by the outside environment. However, seed germination may have been delayed by cold spring temperatures. Germination did not begin until early July. Temperatures measured in late June indicated that only the mound seedbed

(13.4°C) fell within the ideal temperature range for white spruce germination (13-21°C) reported by Fraser (1971). A preliminary count in July indicated that the screef seedbed had very low germination. This delay may have been a result of low temperature (although the normal seedbed was not similarly affected). Late germination may affect a seedling's ability to survive overwinter.

The June temperature relationship to planted germinant survival suggests that once seedlings pass the cotyledon stage, spring soil temperature may have a bearing on subsequent growth and survival. The lack of a strong relationship between August-root zone temperatures and planted germinant survival suggests that temperature may not have been limiting to growth and survival later in the season.

Low temperatures can lead to water stress, affecting a seedling's ability to take up water (Goldstein et al. 1985; Grossnickle 1988; Kaufmann 1975). Low temperatures may also reduce a seedling's ability to photosynthesize (Brand 1990). Soil temperatures less than 9°C can lead to significant increases in water flow resistance for white spruce seedlings in northern Alaska (Goldstein et al. 1985). In Ontario, the sharpest resistances to water flow, in white spruce seedlings, may occur at soil temperatures below 7°C (Grossnickle 1988). Average June-root zone temperatures on the screef and normal seedbeds were less than 9°C and therefore, spring root-zone temperatures may have limited planted germinant survival on

these seedbeds. Higher June root-zone temperatures on the mound, log, and exposed seedbeds may have been more favourable for planted germinant survival. It was noted that the screef seedbed formed a depression allowing water to collect, keeping the seedbed saturated and cold.

The average moist strengths of 495 KPa and 677 KPa, on the normal and screef seedbeds respectively, may have restricted root growth and affected planted germinant survival. Soil strengths above 470 KPa restrict establishment of first year conifer seedlings, but once established, strengths above 140 KPa limit root penetration (Zisa et al. 1980). High June-root zone temperatures on the exposed seedbed appear to have ameliorated the effect of high moist strength on planted germinant survival. The critical penetrometer pressure for root growth of wheat has been found to rise steadily with increases in soil temperature from 10 to 20°C (Greacen 1977).

The relationship of soil strength to planted germinant survival might have been more pronounced if periods of drought had occurred during the first growing season. The drier soil strength measurements in 1994 indicated that average strengths had increased by 2-5.3 times. The only unaffected seedbed was the log which had the same strength. The rotting log seedbed appeared to have high macroporosity which may mean it has low cohesion when moist or dry. Also, a rotting log may retain moisture during drying periods. This implies low strength and

an advantage for root growth and survival on rotting logs during prolonged periods of drought. The mound seedbed still retained relatively low strength compared to the remaining seedbeds. This suggests that the mound may still be a suitable seedbed during brief dry weather (one or two weeks without rain).

Even though drought did not occur, water would likely become a limiting factor for seedling growth and survival in other years. Several studies report rotting logs to be better conservers of moisture than humus or mineral soil (Barr 1930, Place 1950, Harvey et al. 1978). In a mature U.S.A. northern rocky mountain forest, spring to fall moisture contents range from 118.1% to 244.4% o.d.w. (oven dry weight) for decayed wood, 74.2% to 141.*% o.d.w. for humus, and 27.9% to 40.8% for mineral soil (Harvey et al. 1978). Similar patterns occur in mature forests of central British Columbia (Barr 1930). Spring to fall moisture content of decaying wood ranges from 62% to 537% o.d.w., whereas, the moisture content of exposed mineral soil ranges from 5.8% to 61.7% o.d.w.. However, higher moisture content in rotting logs does not necessarily mean more available water. In the boreal forest humus may reach the wilting point during a period of drought, whereas, rotting logs may retain enough moisture to avoid the wilting point (Place 1950).

The forest floor may be the driest seedbed during periods of drought. Both sites two and three had an L+F thickness

greater than 5 cm. This may be enough to prevent root growth into the moisture-holding H layer. This suggests that at least on some occasions white spruce germinants in the boreal forest will be unable to survive on the forest floor during periods of drought.

It was evident that both seed establishment and planted germinant survival were affected by site conditions and by other seedbed properties that were not measured. Overstory cover appeared to have negatively impacted both seed establishment and planted germinant survival on site two. It is possible that high crown cover, combined with understory cover, restricted available light to the point where it was detrimental to seedling survival. Aspen dominated stands with high tree crown covers may be unsuitable for understory establishment of white spruce.

Other factors which may have had an effect on seed establishment and planted survival are: aeration, damping off fungi, nutrition, and leaf smothering. Decreasing levels of oxygen are related to increased mortality, and reduced foliar nitrogen and root length in white spruce seedlings (Zinkan et al. 1974). The screef seedbed may have had low aeration due to water accumulating in the depressions. It was apparent that the log seedbed had high macroporosity which should have allowed for favourable aeration. However, Rowe (1955) noted that white spruce seedlings growing on decayed wood had poor root growth. The mixing of soil in the mound seedbed appeared

to have decreased bulk density and added increased microporosity which should have also allowed for improved aeration.

Damping-off of young seedlings is caused by a variety of weakly parasitic fungi that are normally found in organic debris. These fungi prefer shaded, moist conditions (Smith 1986) which prevail in the understory environment. The screef seedbed, which collected water and leaf litter, may have been particulary susceptible to attack by damping-off fungi (although it was difficult to tell if attack did occur). Rotten logs may be very acidic, and therefore, less prone to mortality from damping-off fungi (Baldwin 1927).

White spruce requires at least moderate fertility for growth (Klinka et al. 1989, Sutton 1969). The log seedbed may have had reduced available mineralized nitrogen and phosphorous (Day 1963). However, this may be compensated by asymbiotic nitrogen fixation (Baines and Millbank 1978; Cornaby and Waide 1973; Granhall and Lindberg 1980; Jurgensen et al. 1984, 1987; Larsen et al. 1978; Roskoski 1980) and the import of nitrogen and phosphorus to seedlings from ectomycorrhizal associations (Baldwin 1927; Harvey et al. 1976, 1978, 1979; Kropp 1982).

It was evident that leaf litter from the previous year caused some mortality to seedlings, particularity on the screef seedbed. Litter was blown into the depressions and then compacted by rain, crushing the seedlings. Rowe (1955)

and Waldron (1959) also noted high mortality of white spruce seedlings from leaf crushing in depressions. Leaf crushing may be critical for seedling survival within the first few months after germination. Chapter III indicates that very little leaf litter accumulated on the log and mound seedbeds.

Table 2-1. Site Description. For species comp. (composition), A = Trembling aspen, Pb = Balsam poplar, and Bi = White birch, with subscripts referring to percent basal area of each species. For site assoc. (association), LBC refers to the Lower Boreal Cordilleran ecoregion of Alberta, Canada, (Corns and Annas 1986) and the number and letter combination refer to a site association within the ecoregion. The → signifies a transition between two site associations.

Site	Basal Area (m^2/ha)	%Crown Cover	Species Comp.	Height (m)	Age	Site Assoc.	L+F Humus Depth (cm)
1	43.5	40	$A_{86}Pb_{14}$	14.6	43	LBC 5c	5
2	40.5	50	$A_{85}Bi_{11}Pb_{3}$	18.1	51	LBC 5c → 4c LBC 5c → 5d	6 to 9
3	39	45	$A_{84}Bi_{8}Pb_{8}$	20.9	52	LBC 5c → 5d	4
4*	(1)19.5 (2)15.0	(1)23 (2)22	(1)$A_{67}Pb_{33}$ (2)$A_{78}Pb_{22}$	(1)15.6 (2)21.1	(1)43 (2)71	LBC 6 → 5d	2

*Two layered stand resulting from burn in 1950 that left part of a stand remaining.

Table 2-2. Anova Table. B_i = Individual observation for a seedbed. B_m = Mean of all observations for a seedbed.

Source of variation	D.F.	Expected Mean Square
Site (S)	3	$5\sigma^2PS + 50\sigma^2S$
Plot within Site (PS)	36	$(5\sigma^2PS)^A$
Seedbed (B)	4	$\sigma^2BPS + 10\sigma^2BS + 40(\sum(B_i - B_m))/5$
Seedbed × Site (BS)	12	$(\sigma^2BPS + 10\sigma^2BS)^B$
Seedbed × Plot within Site (BPS)	144	$(\sigma^2BPS)^C$
Total	199	

[A]Error term for testing Site effect.
[B]Error term for testing Seedbed effect.
[C]Error term for testing Seedbed × Site effect.

Table 2-3. Summary of ANOVA ($P > F$) for site, seedbed, and interaction effects for different physical variables.

Response variable	Source of Variation		
	Site	Seedbed	Site×Seedbed
Temperature Late June, 1993	0.2753	0.0001	0.1394
Temperature Aug., 1993	0.0001	0.0001	0.0001
Soil strength Moist periods, 1993	0.0001	0.0006	0.0001
Soil strength Drier periods, 1994	0.0001	0.0098	0.0084
Vegetation cover Aug., 1993	0.1834	0.0001	0.0956

Table 2-4. Improvement test statistics, and *P* values for the stepwise logistic model-building process, using individual results of first summer seedling establishment of seed and survival of planted germinants. Effects entered in order of which has lowest *P* value for G test statistic.

Seedling	Effect added	Simpler model	G test[1] statistic	Δ DF	*P*[2] value
Planted	Site	Null	132.43	3	<0.001
	Seedbed	Site	141.40	4	<0.001
	Site×Seedbed	Site + Seedbed	24.79	12	<0.025
	ST1[3]	Site + Seedbed + Site×Seedbed	6.11	1	<0.025
	T1[4]	Site + Seedbed + Site×Seedbed + ST1	0.03	1	>0.90
	T2[5]	Site + Seedbed + Site×Seedbed + ST1	0.46	1	>0.50
	V[6]	Site + Seedbed + Site×Seedbed + ST1	0.00	1	>0.95
	Seedbed×ST1	Site + Seedbed + Site×Seedbed + ST1	2.28	4	>0.50
	Site×ST1	Site + Seedbed + Site×Seedbed + ST1	0.69	3	>0.75
Seed	Site	Null	22.64	4	<0.001
	Seedbed	Site	31.73	3	<0.001
	Site×Seedbed	Site + Seedbed	15.32	12	>0.100
	V	Site + Seedbed	1.24	1	>0.250
	T1	Site + Seedbed	0.08	1	>0.75
	T2	Site + Seedbed	1.03	1	>0.250
	ST1	Site + Seedbed	0.00	1	>0.950

[1]G = -2(ln likelihood of model with effect added - ln likelihood of simpler model).

[2]*P* value for testing whether the added effect significantly improves the goodness of fit.

[3]ST1 = Soil strength, moist periods, 1993.

[4]T1 = Temperature, late June, 1993.

[5]T2 = Temperature, August, 1993.

[6]V = Percent vegetation shading (shrubs and herbs), August, 1993.

Table 2-5. Analysis of physical effects on first summer survival of planted germinants and establishment of seed using a stepwise logistic model-building process with improvement test statistics and *P* values.

Seedling	Effect Added	Simpler Model	G test[1] statistic	Δ DF	*P*[2] value
Planted	T1[3]	Null	63.92	1	0.0001
	T1	Site	98.13	1	<0.001
	T1	Seedbed	4.25	1	<0.050
	T1	Site + Seedbed	0.28	1	>0.500
	T2[4]	Null	6.60	1	0.0102
	T2	Seedbed	46.21	1	<0.001
	T2	Site	78.45	1	<0.001
	T2	Site + Seedbed	0.00	1	>0.950
	ST1[5]	Null	51.50	1	0.0001
	ST1	Site	50.48	1	<0.001
	ST1	Seedbed	9.718	1	<0.005
	ST1	Seedbed + T1	3.92	1	<0.050
	ST1	Seedbed + T2	44.58	1	<0.001
	ST1	Seedbed + Site	143.39	3	<0.001
	ST1	Seedbed + T1 +	5.58	4	>0.100
	Site	T1 + T2 + ST1	104.79	3	<0.001
	Seedbed	T1 + T2 + ST1 +	41.86	4	<0.001
	Seedbed ×	T1 + T2 + ST1 +	27.37	12	<0.010
Seed	V[6]	Null	12.94	1	0.0003
	V	Site	15.76	1	<0.001
	V	Seedbed	0.53	1	>0.250
	Site	V	25.47	3	<0.001
	Seedbed	V + Site	15.97	4	<0.005
	Site ×	V + Site +	15.32	12	>0.250

[1]G = -2(ln likelihood of model with effect added - ln likelihood of simpler model.
[2]*P* value for testing whether the added effect significantly improves the goodness of fit.
[3]T1 = Temperature, late June, 1993.
[4]T2 = Temperature, August, 1993.
[5]ST1 = Seedbed strength, moist periods, 1993.
[6]V = Percent vegetation shading (shrubs and herbs), August, 1993.

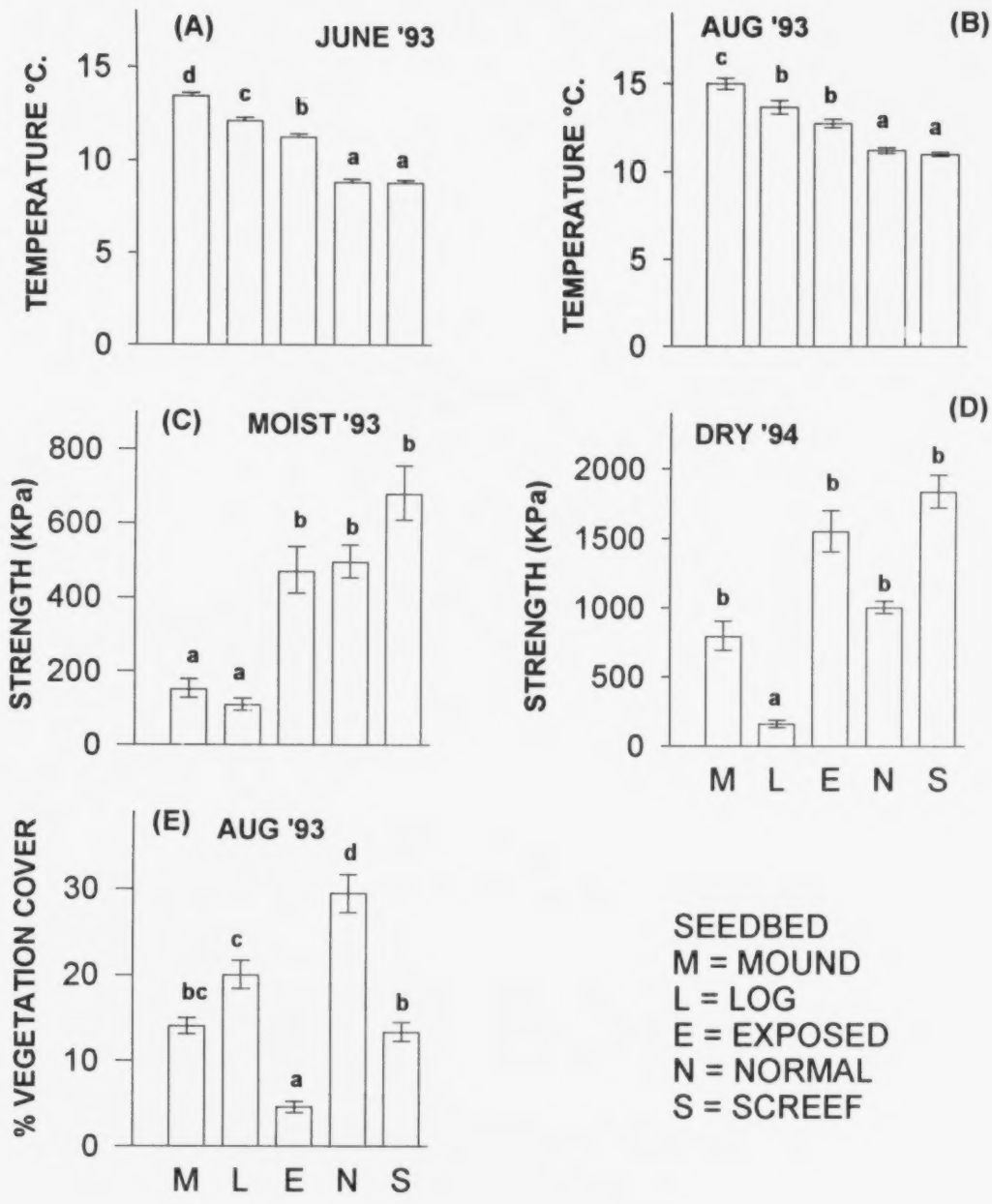

Figure 2-1. Seedbed temperatures in late June 1993 (A) and August 1993 (B), seedbed strength during moist conditions in June and August 1993 (C) and drier conditions in July and August 1994 (D), and percent vegetation cover in August 1993 (E). For any one graph, seedbeds marked with the same lower case letter are not significantly different.

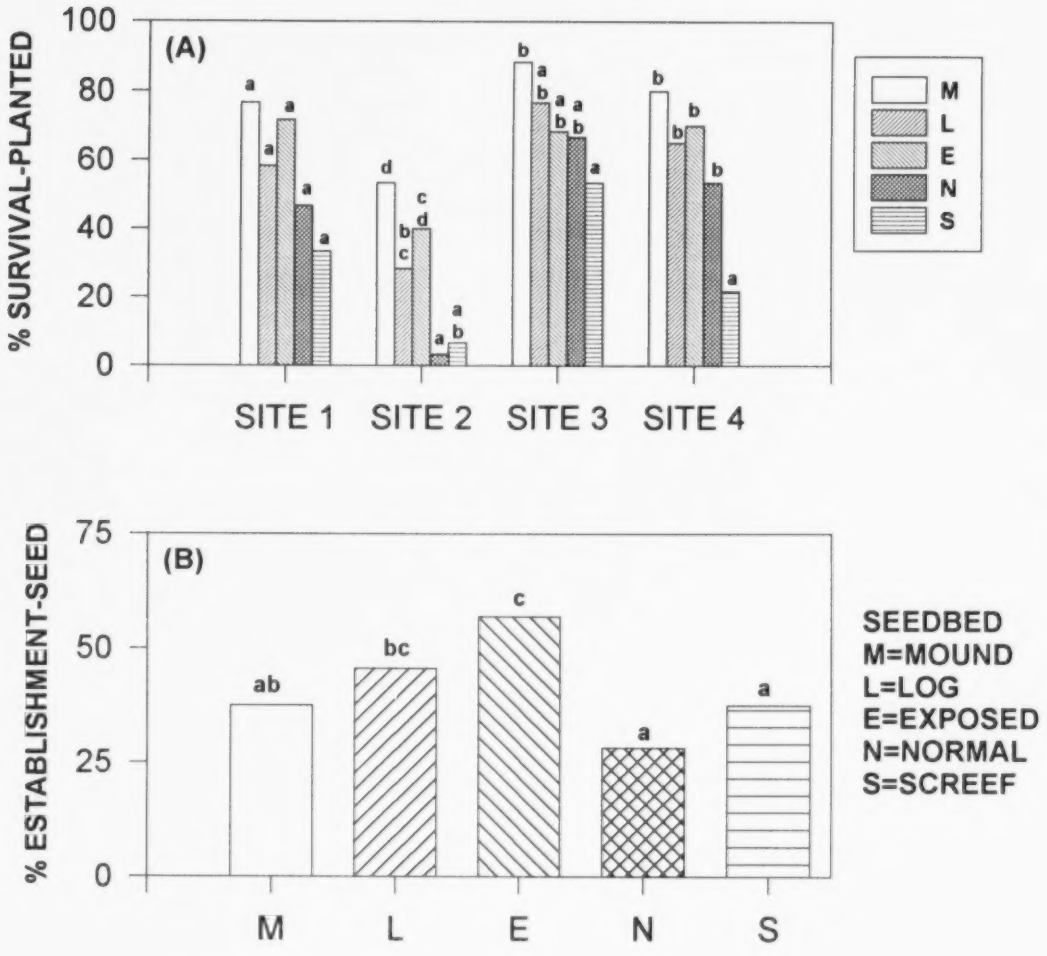

Figure 2-2. First year survival of planted germinants (A) by site and seedbed and establishment of seed (B) by seedbed. Establishment of seed includes germination success and subsequent survival for the first year. For each site on graph (A) and for graph (B) seedbeds marked with the same lower case letter are not significantly different.

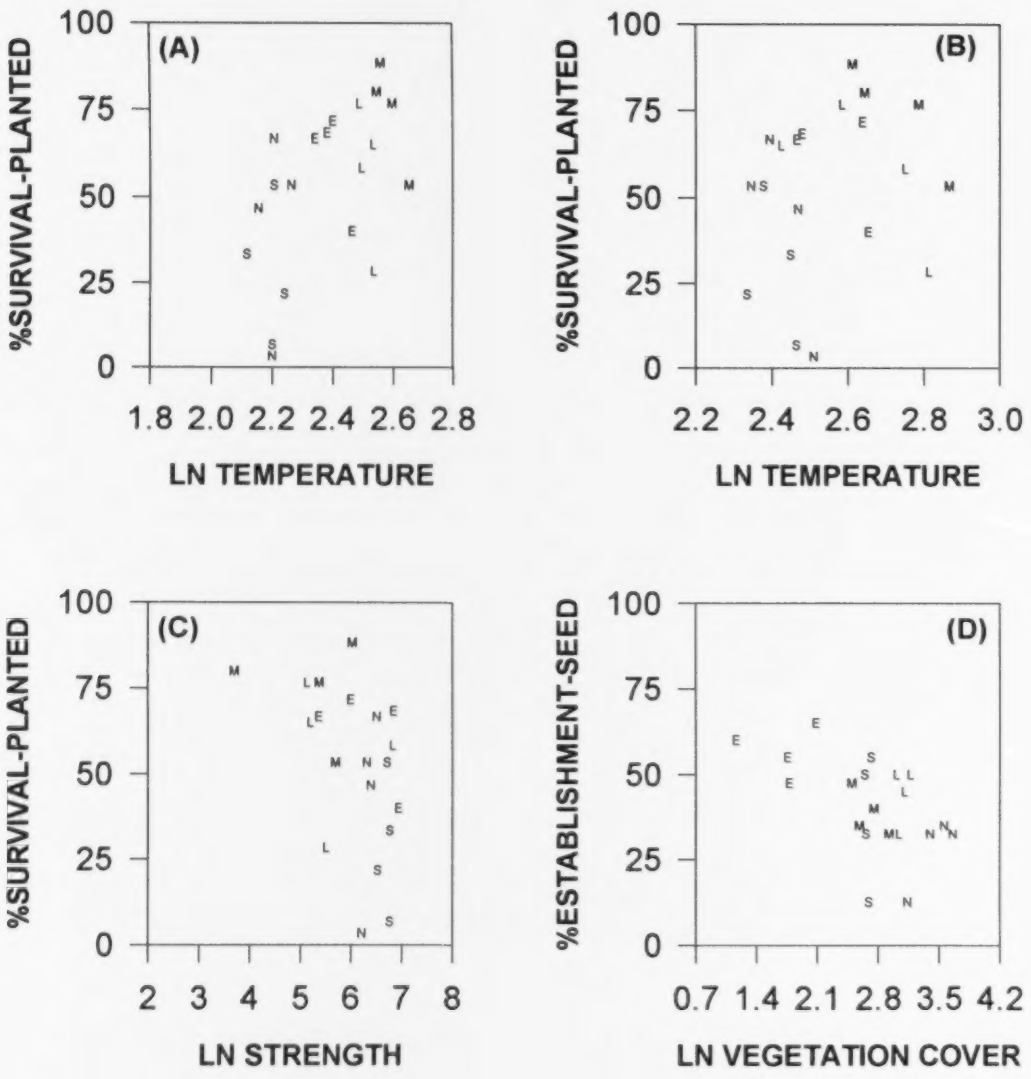

Figure 2-3. Univariate logistic regression analysis showing the relationship between root-zone temperatures in late June 1993 (A), August 1993 (B), and soil strength during moist weather in June and August 1993 (C) with first year survival of planted germinants; and the relationship of percent vegetation cover in August 1993 (D) with first year establishment of seed (includes germination success). Data was plotted by taking the averages for each seedbed on each site. M = Mound, E = Exposed, L = Log, N = Normal, and S = Screef. Sites are not indicated.

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CHAPTER III
The effects of microsite on first year overwinter survival of white spruce beneath aspen dominated boreal mixedwood forests.

INTRODUCTION:

There has been a renewed interest in mixedwood management and partial cut silviculture systems in the boreal forests of Alberta (Brace and Bella 1988; Navratil et al. 1994). One of the objectives is to promote and take advantage of natural regeneration of white spruce (Picea glauca (Moench) Voss) in the understory. Greater success might be gained by understanding the microsites and conditions that promote regeneration in the understory.

The majority of white spruce regeneration on unscarified forest floors, in selectively cut mixedwood forests in Alberta, occurs on rotten wood (Lees 1964, 1970). Rotten wood, in undisturbed mixedwood stands in Manitoba and Saskatchewan (Phelps 1948) and Ontario (Hughes 1967), also supports the majority of white spruce regeneration.

Leaf litter damage may be the major source of overwinter mortality to white spruce seedlings in their first few season of growth and therefore, low leaf litter accumulation on rotting logs may partially explain the high establishment of white spruce on these microsites (Rowe 1955). Wind tends to sweep leaf litter off the tops of small ridges and hummocks (Koroleff 1954) such as rotting logs. Gregory (1966) demonstrated enhanced survival of covered white spruce

seedlings through the first four growing seasons beneath a fully stocked white birch (Betula papyrifera Marsh.) stand. However, he did not have a replicated experiment.

Seedlings established on artificial mounds in mixedwood understories may also have an advantage in survival. These are also raised microsites in which leaf litter would not be expected to accumulate and cause damage.

There is little information about the influence of microsite on leaf litter accumulation and overwinter survival of first year white spruce seedlings in mixedwood understories. This study had three objectives:

1. Determine the amount of leaf litter collected on various seedbeds (microsites): rotting logs, mineral soil mounds, large patches of exposed mineral soil, small patches of exposed mineral soil, and the undisturbed forest floor.
2. Determine seedbed differences in first year overwinter survival of white spruce seedlings established form seed and planted germinants.
3. Determine the association of leaf litter accumulation with overwinter survival of seedlings established from seed and planted germinants.

METHODS:

Site selection and description, plot description, seedling production, and first year field establishment are as outlined in chapter II.

FIELD MEASUREMENT:

LEAF-FALL:

Leaf-fall was measured from October 13 to October 15, 1993 after 95% of leaves were off the deciduous tree. The layers of newly fallen leaves, skewered by a two millimetre thick stick, were counted at each of 10 locations on each seedbed ensuring that no fallen leaves were missed. The results were then expressed as average layers of leaf litter accumulation for that given seedbed.

OVERWINTER SURVIVAL:

Only seedlings that had survived the first summer in either a medium or good condition were selected for this study. These seedlings were straight and had healthy green foliage. Seedlings were established both from planted germinants and from seed. Site two experienced poor establishment and survival and was omitted. Seedbeds were sampled unequally since some experienced poor first year survival.

Prior to leaf-fall, on September 20 to September 22, 1993, plastic glasses (5 cm in diameter by 7 cm high) were secured over a random selection of half of the seedlings. The glasses were secured by hooking bailing wire through the glass into the ground. The other half of the seedlings were left uncovered. Attempts were made to ensure that each seedbed had equal numbers of protected and unprotected seedlings.

On May 3 to May 6, 1994 the overwinter survival was recorded.

WIRES:

Prior to leaf-fall, on September 20 to September 22 1993, 8 cm pieces of 26 gauge copper magnet wire were vertically inserted to a depth of 2 cm (an additional 1.5 cm on the buried end was bent 90° in order to secure) at each of the 10 locations on each seedbed. A length of 1.5 cm was bent 90° at the top of each wire producing a horizontal section that was 3 cm high.

On May 3 to May 6, 1994 the amount that each wire was bent was recorded as either 0°, 45°, or 90°. The data were assigned scores such that 0°=1, 45°=2, and 90°=3. The 10 scores were totalled for each seedbed, at each plot, at each site.

RESULTS:

The screef seedbed had higher leaf accumulation (6.26 layers) than any other seedbed (Figure 3-1). The mound (1.17 layers) and the log seedbeds (1.57 layers) had lower accumulation than the exposed (2.63 layers) and normal (2.82 layers) seedbeds. There were significant site (P = 0.0029), seedbed (P = 0.0001), and site×seedbed (P = 0.0394) effects for leaf layers (Table 3-1). The screef seedbed is obviously different from the other seedbeds and is not included in the analysis (because it had high variability and its inclusion

would violate some of the assumptions for the analysis of variance).

When the screef seedbed was included in the analysis (variances between sites were not significantly different and therefore, no assumptions for the analysis of variance of sites were violated when the screef seedbed was included) with the other seedbeds, there were still significant site effects (P = 0.0005) (not shown). Site two had higher leaf accumulation (3.32 layers) than all other sites (not shown). Site one had lower accumulation (2.58 layers) than site three (2.91 layers) but was not significantly different from site four (2.76 layers). Sites three and four were not significantly different. Leaf layer accumulation serves as a leaf area index for each site and can be used to indicate overstory shading.

There were significant site (P = 0.0001), seedbed (P = 0.0006), and site×seedbed effects for wire bending scores (Table 3-1). The screef seedbed had a higher score (20.8) than all other seedbeds (Figure 3-2). The scores for the mound (15.80), log (15.15), exposed (15.95), and normal (18.08) seedbeds were not significantly different. The scores for sites four (18.7), two (17.8) and one (17.3) were not significantly different. The lowest bending score occurred on site three (14.8).

Seedbed and cup contributed significantly to seedling survival (P < 0.001). The site (P > 0.750), seedbed×cup (P >

0.500), and seedling ($P > 0.250$) terms did not significantly improve the model. Therefore, seedbed and cupped versus uncupped comparisons on overwinter survival were made using the unsaturated model containing only the seedbed and cup effects.

The probability of survival was greater ($P = 0.0001$) for cupped than for uncupped seedlings. The survival for cupped seedlings was 89.7% compared to 75.1% for uncupped seedlings. Multiple comparisons (Figure 3-3) indicate that the probability of survival was lower on the screef seedbed than all other seedbeds. The probability of survival on the normal seedbed was lower than that for the mound, log, and exposed seedbeds. There were no significant differences for the probability of survival between the mound, log, and exposed seedbeds. The survival on the screef seedbed was 47.83% compared to 73.26% for the normal, 89.72% for the log, 91.67% for the exposed, and 93.40% for the mound seedbeds.

DISCUSSION:

The low leaf litter collected on the mound and log seedbeds suggests that leaves fall off or are blown off these seedbeds. The screef seedbed formed a depression which allowed large amounts of litter to accumulate. The significant cupping effect, in the best fit logistic model, suggests that some overwinter mortality to first year white spruce seedlings may be caused by leaf-fall. However, the

lack of a significant seedbed×cup contribution to the best fit logistic model suggests that overwinter survival was similarly reduced on all seedbeds when they were left unprotected by cups. The wire bending experiment tend to support these observations. Wires on all seedbeds were bent to a large degree, however, the amount of bending was equal for all but the screef seedbed. The high bending on the screef seedbed was likely due to the large accumulation of leaf litter. It is possible that the wires did not represent seedlings that well or that seedlings on the screef seedbed were simply able to survive being bent from leaf-fall and snowpress.

The high amount of leaf litter collected on site two may explain the poor first summer establishment for planted germinants and seeded germinants on this site in 1993 (Chapter II). A high litter accumulation means a high leaf area index which indicates a high tree crown cover. The high crown cover may have limited light and reduced establishment on site two during the first summer. The high litter on site two did not appear to affect the wire bending score. Again wires may not have represented seedlings that well. No overwinter survival information was collected for site two.

High snowfall in the winter of 1993/94 may have been the major cause of the difference in overwinter survival between cupped and uncupped seedlings. Snow should have affected each seedbed equally. A large snow effect may have hidden any seedbed differences caused by leaf-fall. However, survival

was still high for unprotected seedlings.

Several reports have suggested that high survival rates of white spruce seedlings are associated with low litter-fall accumulation on raised microsites such as mounds and rotten logs (Kabzems and Lousier 1992; Place 1955; Rowe 1955). The current study also indicates a relationship. The mound and log seedbeds (raised microsites) show high overwinter survival and low leaf-fall. However, these relationships appear to be coincidental. At least in the year examined it is likely that differences in seedbed overwinter mortality were caused by factors other than leaf damage. Rotten logs are the common seedbed for regeneration beneath conifer stands (Griffith 1931) in central British Columbia and on subalpine cutover stands in southwestern Alberta (Day 1964). Conifer needles would not be expected to supply the same damaging effects to young seedlings as deciduous leaf litter would. Therefore, there must be other factors which favour regeneration on rotting logs.

The seedbed comparisons of overwinter survival are similar to those observed for first year survival of planted germinants (Chapter II). The results from this study suggested that root-zone temperatures and moist soil strength were related to first year survival. It was noted that damping-off fungi, and seedbed aeration and nutrition could have also affected first year survival. It is likely that one or more of these factors caused stresses in many of the

seedlings. These stresses were undetected morphologically. Furthermore, seedlings in the normal and screef seedbeds likely suffered more stress. This may explain the seedbed differences in overwinter survival.

It is possible that much of the damage attributed to leaf-litter occurs during the first growing season. In August, 1993 it was observed (Chapter II) that many of the first year seedlings had been smothered and crushed by windblown litter that settled. This was particulary noticeable on the screef seedbed where it was apparent that some mortality from leaf-litter smothering did occur. As noted, this seedbed allows leaf-litter to accumulate because of the depression formed. Rowe (1955) and Waldron (1966) also noted that depressions (furrows) allowed leaves to collect and cause mortality. However, their observations were on two and three year old white spruce seedlings.

This study indicates that leaf litter did not have a significant role on microsite differences in first year overwinter mortality. However, there may be other important considerations such as the amount of leaf litter damage caused by blowing leaves (from the previous fall) which may settle on young germinants during their first growing season. Also blowing litter may cause damage in the second season when it is added to existing litter layers that are covering seedlings. There is a need for further research.

Table 3-1. Summary of ANOVA ($P > F$) for site, seedbed, and interaction effects for different response variables.

Response variable	Source of Variation		
	Site	Seedbed	Site×Seedbed
Leaf Layers Oct. 1993	0.0029	0.0001	0.0394
Wire bending score May 1994	0.0001	0.0006	0.0133

Table 3-2. Improvement test statistics, and P values for the stepwise logistic model-building process, using experimental results of overwinter survival of cupped and uncupped seedlings (originating from seed and from planting). Effects entered in order of which has lowest P value for G test statistic.

Effect added	Simpler model	G test[1] statistic	Δ DF	P[2] value
Seedbed	Null	65.78	4	<0.001
Cup	Seedbed	21.49	1	<0.001
Seedling	Seedbed + Cup	3.79	1	>0.250
Seedbed×Cup	Seedbed + Cup	5.02	4	>0.500
Site	Seedbed + Cup	0.53	2	>0.750

[1]G = -2(ln likelihood of model with effect added - ln likelihood of simpler model).

[2]*P* value for testing whether the added effect significantly improves the goodness of fit.

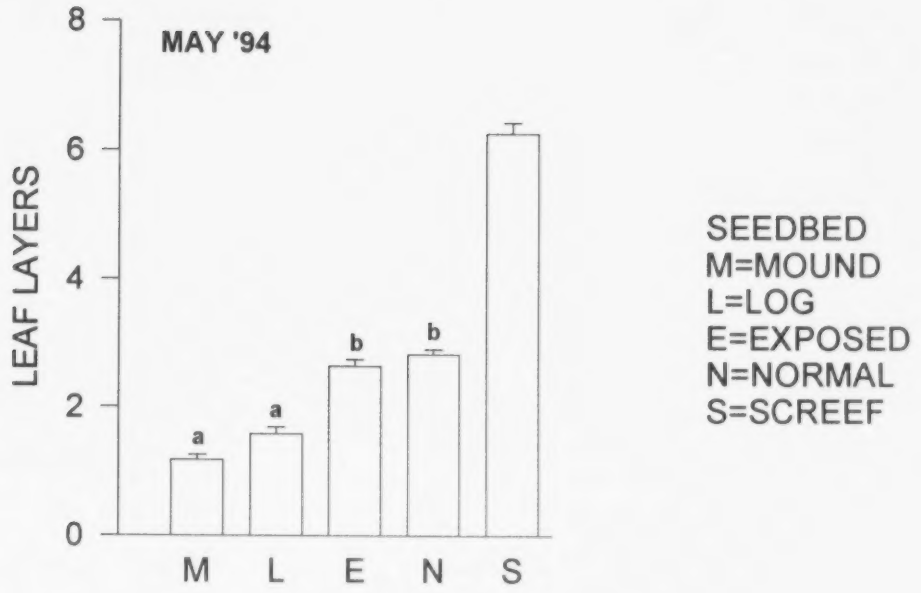

Figure 3-1. Mean number of leaf layers on seedbeds and standard error bars. Seedbeds with the same lower case letters are not significantly different. The screef seedbed is obviously different from the other seedbeds and was not included in the analysis (because the seedbed has high variability and inclusion would violate some of the assumptions for the analysis of variance) but is still presented.

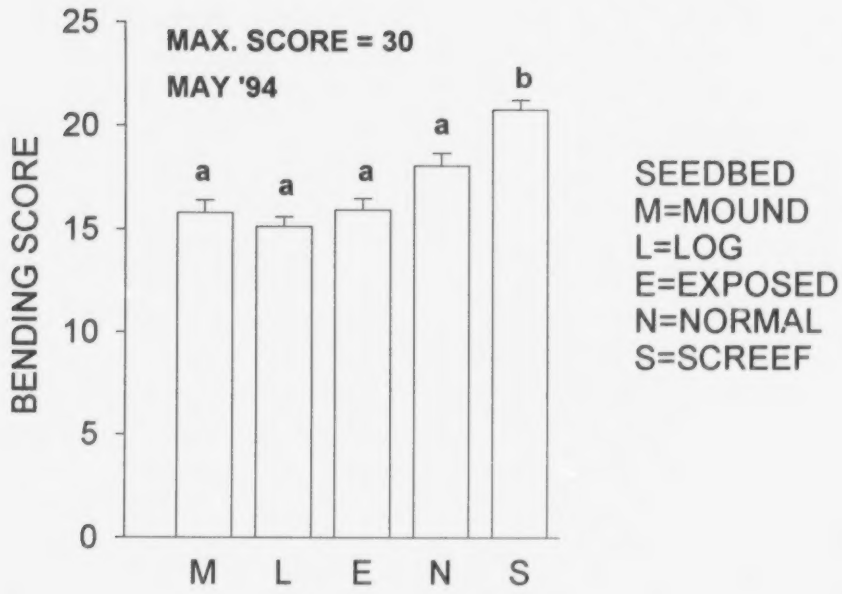

Figure 3-2. Mean bending score (with standard error bars) of wires on different seedbeds due to leaf-fall and snowpress. Seedbeds with the same lower case letters are not significantly different.

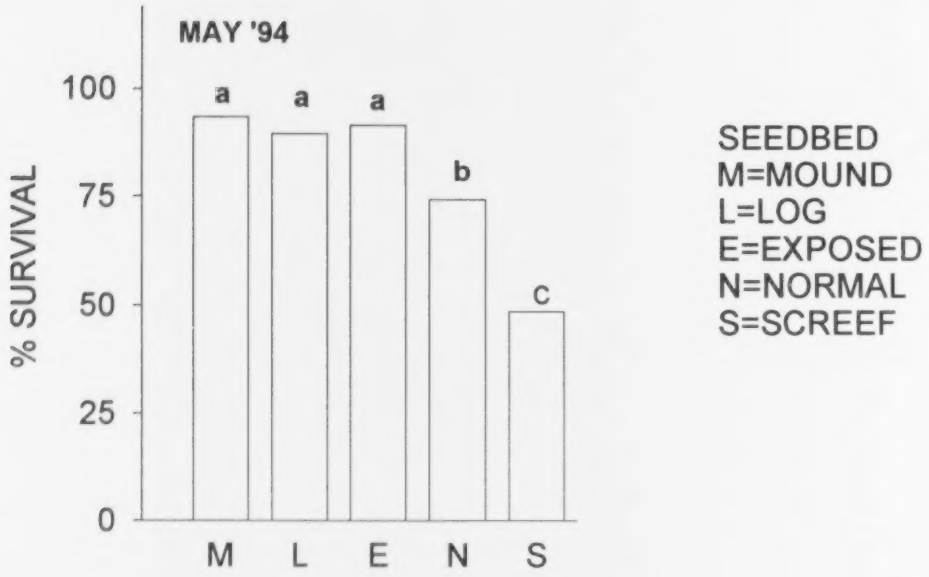

Figure 3-3. Mean percent overwinter survival on different seedbeds. The odds of survival on seedbeds marked with the same lower case letter are not significantly different.

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CHAPTER IV

GENERAL CONCLUSIONS:

Mounds or exposed mineral soil (large patch disturbance) may promote natural or artificial seeding of white spruce beneath 40-70 year old aspen dominated boreal forests. Rotting logs may also be favourable seedbeds, although, it would be difficult to create this seedbed on an operational basis. The undisturbed forest floor and screef (small patch mineral soil exposure) seedbeds are not recommended. Both of these microsites were associated with poor first summer seed establishment, first summer planted germinant survival, and first year overwinter survival. First summer seeding establishment on the mound seedbed might have been improved if seed were deposited on a more soil erosion resistant surface.

In comparison to the normal forest floor, mineral soil exposure (exposed seedbed) reduced understory vegetation cover, raised spring temperature, improved seeded first summer establishment, tended to increase planted germinant first summer survival, and gave higher first year overwinter survival. Mounding raised spring temperature, lowered impedance to root growth in moist conditions, reduced fall leaf litter accumulation, tended to increase planted germinant first summer survival, and gave higher first year overwinter survival.

The complete removal of understory vegetation on the exposed seedbed likely increased the amount of far red light

reaching the forest floor. Far red light stimulates seed germination of unstratified seed (Carlson 1983). This could at least partially account for the high seeded establishment on this seedbed.

The planted germinants simulated seedlings that had germinated and grown beyond the cotyledon stage. Growth of these seedlings was under direct environmental control (as opposed to growth controlled by seed reserves for the seeded germinants). The warm June root-zone temperatures on the exposed, mound and log seedbeds may have aided survival. Cold temperatures can increase the viscosity of water affecting a seedling's ability to take up water (Goldstein et al. 1985, Grossnickle 1988, Kaufmann 1975). Low temperatures may also affect a seedling's ability to photosynthesize (Brand 1990). The screef and normal seedbeds may have been at a disadvantage. Soil in the normal seedbed was insulated by humus thus reducing warming in the spring. The screef seedbed was usually a depression where water accumulated, leading to saturated conditions (due to a very wet spring) and cold temperatures.

The low moist soil strengths on the log and mound seedbeds also may have helped planted germinant survival. Average strengths of 495 KPa and 677 KPa, on the normal and screef seedbeds respectively, may have restricted root growth resulting in low survival. Soil strengths above 470 KPa restrict establishment of first year conifer seedlings, but

once established, strengths above 140 KPa limit root penetration (Zisa et al. 1980). The high June root-zone temperatures on the exposed seedbed may have compensated for high moist soil strength. Greacen (1977) reported that the critical penetrometer pressure for root growth of wheat rose steadily with increases in soil temperature from 10 to 20°C.

The low number of litter layers collected on the mound and log seedbeds suggest that leaves are blown off or fall off these seedbeds. However, overwinter survival was similarly reduced on all seedbeds when left unprotected by cups. This suggests that differences in leaf litter accumulation between seedbeds were not related to differences in overwinter survival.

It appeared that higher survival was due more to favourable growing conditions (ie, high June root-zone temperatures and low moist soil strength) during the summer. Seedlings growing on the screef and normal seedbeds may have been weakened by physiological stresses that were not detected morphologically. It is possible that some of this stress may have been caused by old leaf litter from the fall of 1992. It was observed that some old litter was blown around and settled on the young seedlings. This litter became compacted with the high amount of rain. The screef seedbed accumulated a large amount of litter and some first summer mortality did occur as a result. Those seedlings that did survive may have been weakened either due to crushing or shading. The normal

seedbed also appeared to be affected. The removal of the old leaf litter may have reduced damage on the exposed seedbed.

Protected seedlings did experience higher overwinter survival than unprotected seedlings. However, this appeared to be due to snow press rather than leaf litter damage. High snowfall occurred in the winter of 1993/94. All seedbeds would have been equally affected by snow.

Thin wires were used to simulate seedlings. The screef seedbed experienced higher overwinter wire bending which could be attributed to high leaf litter crushing. All other seedbeds experienced similar wire bending which further suggests that leaf litter was not a large factor for overwinter mortality. The screef seedbed had very high litter accumulation compared to the other seedbeds yet there was no evidence that the litter lead to higher mortality. It is possible that wires did not simulate seedlings that well or that the seedlings were simply able to survive being crushed.

Removal of the humus layer should improve water availability for germinating seedlings on the exposed seedbed during periods of drought. This may also be true for the mound seedbed. However, the mound was built over an intact humus layer. Humus tends to have coarser pore space than most mineral soils. This would impair water movement from below, during dry periods, since the humus layer would have a lower unsaturated hydraulic conductivity than mineral soil (Örlander 1990). This potential problem could be solved by building the

mounds on bare mineral soil or mixing the humus and mineral soil together as the mounds are built. Future studies should examine how water availability relates to survival on the exposed and mound seedbeds.

Impedance to root growth increased by 2-3 times as the soil became drier. The strength on the mound tended to be lower than the exposed and normal seedbed strengths. This suggests that mixing improves root penetration. This may be very important if moist strength alone limits root penetration and seedling survival on the normal seedbed. The implications are that both the normal and exposed seedbeds would limit root penetration and seedling survival during periods of drought.

It was evident that there were other environmental and site effects controlling first summer seeding establishment and planted germinant survival besides understory vegetation cover, June root-zone temperatures and moist soil strengths. These factors may have also caused stresses to seedlings resulting in overwinter mortality.

High crown cover may have reduced both first summer seeded establishment and planted germinant survival on site two. The high crown cover in combination with understory vegetation may have minimized the amount of available light reaching the forest floor. Also, high leaf fall may be detrimental to overwinter survival. However, high litter did not appear to affect wire bending scores on this site. No overwinter survival information was collected for site two.

Stands with high tree crown covers may be unsuitable for understory establishment.

Soil erosion caused some first summer mortality of seeded germinants on the mound seedbed. Some seed was washed down to the bottom of the mound. Many seedlings that managed to germinate were uprooted or flattened (pointing downhill) by rain. Other factors which may have had an effect on first year establishment and survival are: aeration, damping off fungi, and nutrition.

Future studies should explore how soil temperature, moisture, seedbed strength, and light availability affects seedling survival and growth on the various seedbeds, over a period of a few years. Several measurements should be made throughout each growing season to monitor change in these physical properties. Available nitrogen and phosphorous, and seedbed aeration may also be important factors to examine. Survival, seedling biomass and foliar nutrient analysis would indicate which seedbeds are the more favourable after several years growth.

The implications of this study are that site preparation to build mounds or expose mineral soil may enhance white spruce establishment beneath 40-70 year aspen dominated boreal mixedwood forests. Any activities to increase the amount of well decayed coarse wood debris should also aid establishment. Relatively few white spruce trees should be available to act as a seed source. If not, artificial seeding could be used to

establish regeneration. The process described represents a natural shelterwood system. After the white spruce has grown for 20 years the aspen would be carefully logged using understory protection measures, leaving as many white spruce as possible undamaged (Navratil et al. 1994). Some deciduous trees would grow back and the final harvest would be a conifer-deciduous mix. This process would ensure maximum use of the land base and may also help retain biodiversity and recreational values.

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